

On Periodomorphosis, Iteroparity and Life-Cycles in Males and Females of *Tachypodoiulus niger* (Leach) (Myriapoda, Diplopoda, Julidae) in France, Germany and Great-Britain

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ABSTRACT

In spite of appearances, the cycles and life-history of *Tachypodoiulus niger* have been hitherto poorly known. In the same way as he did previously in *Ommatoiulus sabulosus*, the author describes and interprets the cycles of *Tachypodoiulus niger*, particularly according to VERHOEFF's investigations in Germany, those of FAIRHURST in Great-Britain, and to the author's 38 years of mostly unpublished data and experiments on this species in France, Germany and Great-Britain, and in the light of recent knowledge.

RÉSUMÉ

Sur la périodomorphose, l'itéroparité et les cycles de vie des mâles et des femelles de *Tachypodoiulus niger* (Leach) (Myriapoda, Diplopoda, Julidae) en France, Allemagne et Grande-Bretagne.

En dépit des apparences, les cycles de *Tachypodoiulus niger* sont mal connus. Comme il l'a fait antérieurement pour *Ommatoiulus sabulosus*, l'auteur décrit et interprète les cycles de *Tachypodoiulus niger*. Pour ce faire, il s'appuie sur les investigations de VERHOEFF en Allemagne, de FAIRHURST en Grande-Bretagne, ainsi que sur des données et expériences - pour la plupart inédites - de 38 années de recherches personnelles sur cette espèce en France, en Allemagne et en Grande-Bretagne. Les interprétations ont, de plus, été faites à la lumière de nos connaissances actuelles sur la périodomorphose.

INTRODUCTION

Our current knowledge of the cycles in *T. niger* mainly goes back to the data of VERHOEFF (1915-1934: particularly 1928, 1932) and SAHLI (1966). In collaboration with J. G. BLOWER, FAIRHURST (1968) translated the data of his predecessors into English, mentioned those of HALKKA (1958) and added his own worthwhile observations.

[In reading SAHLI's thesis (1966) the British authors did not understand that in *Tachypodoiulus* (and *Ommatoiulus*) it is possible for a specialist - taking attention to details - to distinguish an intercalary from a juvenile male (cf. SAHLI, 1966): only *extremely rare* cases (say in the region of 1: 500 intercalaries) may constitute exceptions].

SAHLI, F., 1996. — On periodomorphosis, iteroparity and life-cycles in males and females of *Tachypodoiulus niger* (Leach) (Myriapoda, Diplopoda, Julidae) in France, Germany and Great-Britain. In: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. Mém. Mus. natn. Hist. nat., **169** : 373-384. Paris ISBN : 2-85653-502-X.

New investigations were made by the present author from 1966 to 1992, in Burgundy, the French Pyrenees (Ariège), French Alps, Germany and Great Britain. On the one side, these researches and on the other the reinterpretation of VERHOEFF's data and my own prior to 1966, showed that the cycles of *T. niger* were still poorly understood and much more complicated than myriapdologists thought.

[Concerning cycles, periodomorphosis, adult to adult moults and combined strategies, HOPKIN & READ (1992) partly overlook or misinterpret some recent results of the present author, concerning, among others, *Tachypodoiulus* sp., *Ommatoiulus* sp., *Allajulus nitidus* and *Blaniulus guttulatus*].

This paper aims to set the record straight regarding our knowledge of cycles in *Tachypodoiulus niger*.

ADOPTED NOMENCLATURE

The definitions and abbreviations used here have been given in several previous papers (SAHLI 1990a, b, 1991a, b, c) to which the reader is referred.

Concerning the seriations, from reasons of symmetry, and taking into account the intercalary appearance season, the same numbers as those adopted for *O. sabulosus* (i.e. seriation 1: intercalaries s1 in autumn of the year x; seriation 2: intercalaries s1 in spring of the year x+1) will be used for *T. niger* (Table 3). We will add a seriation 3 and 3' specific to *Tachypodoiulus*.

RESULTS

My own cultures, experimental investigations, field observations, along with those of VERHOEFF (*passim*) led to the results recorded in Tables 1-8 and in Figures 1 and 2.

At low altitudes, ad1 production (maturation moults of juvenile to first adult males ad1 = MMJ) can take place (see, among others, Table 7) in the following ways:

- (case a) at the end of the winter/spring of the year x (before mating and egg deposition),
- (case b) at the summer/autumn of the year x (i.e. several months before egg-laying in spring of the year x+1, as it is the case in *Allajulus nitidus*). Nevertheless, mating can additionally take place in autumn of the year x,
- both cases (a and b) in the same year.

In other words, depending on the environmental conditions, *T. niger* is able to use two strategies of ad1 male production (either spring or autumn), or a combination of the two (spring + autumn).

Results concerning seasonal cycles in *T. niger* are recorded in Table 4. This gives the "base cycle" which includes *all fundamental possibilities*. From the 8 basic possibilities (a to h) one can derive all the possible ways, should one wish to go into details and individual cases. From the base cycle all the possible patterns can be reconstituted.

Base cycles have been given for *O. sabulosus* in Burgundy (SAHLI, 1990a, Fig.1) and for Mediterranean populations (SAHLI, 1991a, b, Table 1). [In Sahli (1991, table 1) a forgotten vertical line should connect the ad1 (in case b, seriation 1''β) and the s1 (in case a, seriation 1β) in summer. In the same table, the two vertical unbroken lines must be regarded as two vertical braces].

INTERPRETATION AND DISCUSSION

As in *O. sabulosus*, short standing (SL) and long-standing (LL) intercalaries exist in *T. niger* (SAHLI, 1990b).

Results taking into account the author's experimental data and field observations, as well as VERHOEFF's investigations are recorded in Tables 1 & 2. In the present state of our knowledge, two cases can be distinguished in Germany and Burgundy up to 1000 m altitude: one in lowlands and hills, another in the Allgau mountains (800 m) and in a rock shelter in the Saarland, both in Germany.

As shown in Tables 1 & 2, in the sites under 1000 m, there are two typical possibilities, at least in the present state of our knowledge:

TABLE 1. — The two possible cases in *T. niger*, at an altitude under 1050 m in some German regions (particularly in Saarland) and in Burgundy. SUM = summer.

Case a	SPRING		SUM-AUTUMN
Egg deposition	+		
ad1 production	+	and/or	+
sch ♂ production (ad-sch ♂)			+
ad2 production (sch ♂-ad2)			
- ad2 of SL origin	few		
- ad2 of LL origin			+

Case b	SPRING		SUM-AUTUMN
egg deposition			+(?)
typical ad1 production			+
typical sch ♂ production	+		

TABLE 2. — *T. niger* in Burgundy and some German regions. A: subdivision of ad1. B: typical appearance of sch ♂. In case b', ad1 mating is also possible -(first-) in autumn of year x.

A	Spring	Sum/Autumn
case a : spring ad1 (reproduction = year x)	+	
case b : summer/autumn ad1 (= reproduction year x)		+
case b' : summer/autumn ad1 (= main reproduction year x+1)		+

B	Spring	Sum/Autumn
case a : sch ♂ from ad1 of case a		+
case b : sch ♂ from ad1 of case b	+	

- case a = in Burgundy (at the numerous sites studied) and in epigeal animals from Germany (Saarland, Hunsrück, Eifel, Rheinland, Taunus and Hessen). In this case: (a1) egg laying takes place in spring; (a2) ad1 production in spring and/or autumn; (a3) typical - or majority - sch ♂ production in summer/autumn. Sch ♂ are mainly (or only?) made up of LL and R individuals. The predominance of LL in *T. niger* contrasts with that of SL in Mediterranean *O. sabulosus* and probably in *O. moreleti* in Australia and southern Portugal (BAKER, 1978, 1984).

- case b = in Germany in the Allgau (750-1050 m), at least according to the culture results of VERHOEFF (1934), and in a rock shelter at Wadern in Saarland. In this case : (b1) egg laying(?) and ad1 male production take place at the end of summer/onset of autumn; (b2) sch ♂ are produced in spring. In VERHOEFF's cultures (from 1924 to 1928) only sch ♂ SL (thus an α succession) were observed. (The question of whether this was the result of the culture conditions remains open). A complete absence of LL sch ♂ in the Allgau mountains would be astonishing. In Saar cultures (in a unheated basement - with open windows - of the Saarland University) of individuals collected in the Wadern rock shelter, the following succession has been observed: ad (collected in autumn x) - s (spring x+1) - ss (autumn x+1). A succession β (with R sch ♂) as been obtained instead of the α one (ad—s—ad) of VERHOEFF.

In case a, some sch ♂ (ad-sch ♂) may sometimes be (exceptionally?) produced in spring in Burgundy, as well as in Saarland. If this occur, such sch ♂ (which would be SL ones) could be regarded as minority sch ♂ in comparison with the whole sch ♂ liable to be collected in spring.

Like his predecessors, FAIRHURST (1968, 1974) was unaware of the existence of LL sch ♂. He also did not know about the possibility for adults maturing in autumn to stay adults without moulting until the following spring. He trusted the informations given by VERHOEFF

(*passim*) and HALKKA (1958). For these reasons, it seems that FAIRHURST regarded - at least implicitly - the spring postadult male production (e.g. the passage from males become SL intercalaries 1 in autumn into ad2 males in the following spring) as common, even exclusive (based on the last row of ocelli appeared in animals preserved in alcohol). In the same way, FAIRHURST regarded implicitly the ad-sch♂ moult as common in spring (sch♂ being produced in spring from adults which become adults in the previous autumn).

TABLE 3. — Numeration adopted for the seriations in Burgundy and some regions of Germany. Seriations 1 and 2 - homologous to those 1 and 2 of *T. niger* - exist in *O. sabulosus*.

spring (year x) ad1 ♂♂ (low altitudes: Burgundy, Germany)
SERIATION 1: s1 intercalaries in summer/autumn (year x) (cf <i>O. sabulosus</i>)
summer (year x) ad1 ♂♂ (e.g. in the Allgau mountains)
reproduction period = year x
SERIATION 2: s1 intercalaries in spring x+1
summer/autumn ad1 ♂♂ (year x) (in Germany plains)
typical reproduction period = year x+1
SERIATIONS 3 & 3': s1 intercalaries = at the end of spring or sum/autum year x+1

TABLE 4. — Basic cycle of *T. niger* in Burgundy, Great-Britain and some German regions. **A**: starting from ad1, becoming adults in spring (SP). **B** and **C**: starting from ad1, becoming adults in summer (SUM) /autumn (AUT). SER.: seriation. Unbroken line means a moult. Dotted line means no moult.

	CASE SER	SP x	SUM-AUT x	SP x+1	SUM-AUT x+1
A					
a	1 SL	ad1 —————	s1 —————	ad2	
b	1 LL α	ad1 —————	s1	s1	ad2
c	1 LL β				ss
B					
d	2 SL α		ad1 —————	s1 —————	ad1
e	2 LL β		ad1 —————	s1 —————	ss
C					
f	3α		ad1	ad1 — s1 —	ad2
g	3β		ad1	ad1 — s1 —	ss
h	3'		ad1	ad1 ad1 —	? s1

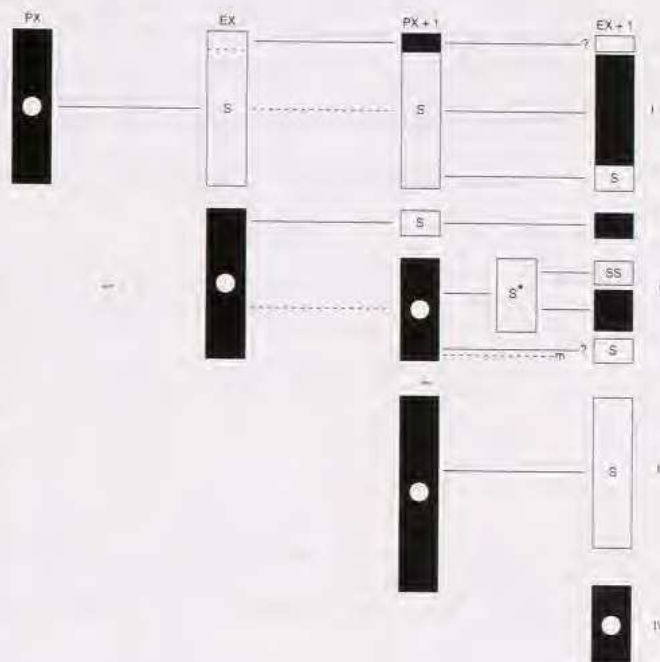
In the present state of our knowledge in Burgundy and in Germany, SL successions never appear as exclusive or even common. From numerous cultured animals in different conditions and during several years, I never obtained spring intercalaries from epigeous adult males (say ad1 or presumed ad2) collected in the previous autumn. I obtained spring intercalaries only from adults collected in the rock shelter at Wadern in autumn (case b). Conversely, sch♂ collected in autumn, as well as as sch♂ (particularly s1 ones) obtained in cultures in summer/autumn, never gave postimaginal adults the following spring in cultures. Only autumn sch♂ from the Wadern's rock shelter gave spring postadult males (case b).

It is possible that spring SL (case b) exist in a more or less high numbers in Great-Britain. Nevertheless, according to my own investigations made at Milldale (G.B.) in 1981 and 1983, the cycle seems to include fundamentally sch♂ LL (case a) as in Burgundy and Saarland. FAIRHURST's observations in Britain require confirmation: the case in Britain needs more

investigations, particularly using cultures. Freshly moulted spring sch♂ might be ss ones (sch♂ in autumn of the year y giving ss in spring $y+1$?).

In both cases (a and b) one can admit the possibility of a double production of LL sch♂ and SL ones (Fig. 1), the number of the SL sch♂ being variable. For instance, the SL may be either few or absent (case a) or more frequent (case b) as in the Allgau mountains (if appearances correspond to realities). Besides his Allgau results, VERHOEFF (1923, 1925) obtained SL in 1922 (an adult collected on 24. 4. 1922 which turned into a SL on 12. 6. 1922 and then into an adult on 15.9.1922).

FIG. 1. — Cycle of males in *T. niger* in Germany and Burgundy. The figure takes into account possibilities of both LL and SL intercalaries. **I**: males which became adl in spring of year x (Px). **II**: males which became adl in summer/autumn x (Ex). In **I** and **II** it is arbitrarily assumed that the number of spring adl (adl = solid rectangles with an open circle; ad2 = entirely solid rectangles) in year x is equal to the number of summer/autumn adl of year x (under this assumption the solid rectangles in Px and Ex are of equal dimensions). **III** and **IV**: new generation (of year $x+1$). In **III** and **IV** it is arbitrarily assumed that the number of spring adl (III) is much higher than the number of summer/autumn adl (IV) (under this assumption the solid rectangles with an open circle are of different dimensions). Sch♂ are represented by open rectangles. Dashed lines: without moult or transformation; solid lines: transformation after a moult. - m: death. ss: double intercalary form. Asterisk: sch♂ at the end of the spring/beginning of summer (after VERHOEFF, 1923).



Bear in mind that two strategies can be used by Mediterranean *O. sabulosus*: type 1 = MMJ at the end of winter/onset of spring, i.e. a long time before egg-laying in summer/autumn; type 2 = MMJ at the end of spring/summer of the year x , just before mating and egg deposition (SAHLI, 1986, 1991a, b, c, 1992). Nevertheless, in *O. sabulosus* MMJ of type 1 or 2 (or both) and egg-laying take place the same year. The respective strategies used by *T. niger* (at low altitudes in Germany and in Burgundy) and *O. sabulosus* in the South-East of France are not strictly superimposable: this is the reason why we speak of cases a and b in *T. niger* and types 1 and 2 in *O. sabulosus*.

In the Département des Hautes-Alpes (1000 - 1600 m) the production of ad. and sch♂ males (collected under snow bridges or stones) might take place as it does in the case a (SAHLI 1970 & unpubl.), at least in the present state of the investigations. In the Pyrénées ariégeoises, the production of ad-sch♂ might correspond to case b, sch♂ being numerous in autumn according to preliminary observations. A thorough study, over numerous years, needs to be carried out in the Hautes-Alpes, in the Pyrénées ariégeoises and in the Hautes-Pyrénées (in which, on the slopes of the Pic de Campbielh, sch♂ as well as ad males are frequent under stones at the end of the summer).

Although simplified, Tables 5 & 6 allow the interpretation of virtually all the innumerable field and culture data accumulated, be it in spring (year $x+2$ in Table 5) or in summer/autumn (year $x+1$, Table 6).

In spring (x+2) the $\text{sch}\sigma$ number will depend of the number of ad1 of year x+1, which were produced in spring x+1. If one supposes, for instance that these ad1 were numerous, the supposed situation will lead to numerous LL, shown in bold type in Table 5.

TABLE 5. — *T. niger* in Saarland and Burgundy. Starting from spring ad1. The predominancy - hypothetically assumed - is expressed in bold type. Concerning $\text{sch}\sigma$, one has assumed (arbitrarily) that the LL (case a) are predominant. Year x+2 will include on the one hand new ad1 (year x+2), assumed (arbitrarily) to be predominant; and on the other hand, mainly slow ad2 (year x) as well as LL (year x+1) (slow ad2 = arising from LL; fast ad2 = arising from SL). The possibilities of ss (from LL in autumn x+1) and the appearance of new ad1 (year x+1) have not been taken into account. aut: autumn; n: new; sp: spring.

spx	aut x	sp x+1	aut x+1	sp x+2
				some fast ad2 (x)
— $\text{sch}\sigma$ (SL) —		some fast ad2	s2	s2 (LL) (x)
				ss (x)
ad1				
— $\text{sch}\sigma$ (LL) —		$\text{sch}\sigma$ (LL)	ad2	slow ad2 (x)
				new ad1 (x+2)
			ad1 n	"old" ad1 (x+1)
				some fast ad2 (x+1)
				$\text{sch}\sigma$ (LL) (x+1)

TABLE 6. — *T. niger* in Saarland and Burgundy. Starting from spring of year x+1. The following autumn, slow ad2 (bold) are assumed (arbitrarily) to be well represented. The number of new autumn (x+1) ad1 is variable: compared with the number of s1 (autumn year x+1), it can be higher (in this case ad1 would be in bold letters) or lower (s1 would be in bold).

spring x+1	autumn x+1
some fast ad2	s2 (x)
$\text{sch}\sigma$ (LL)	slow ad2 (x)
	new autumn ad1 (x+1)
new spring ad1	s1 (x+1)

As a general rule in spring and in case a, the ratio $\text{ad1}/\text{sch}\sigma$ in spring x+2 (Table 5, Fig.1), will depend on:

(a) the number of "new" ad1 (i.e. the number of "new" freshly MMJ) in year x+2, plus the number of possible "old" ad1 from autumn x+1 (MMJ in autumn x+1) which have remained winter ad1 without moulting. These new ad1 can be high, middle or low in number.

(b) the number of LL s1 (which became s1 in autumn x+1). LLs1 in turn depend on the number of ad1 in spring x+1. A few SL s1 (? in Fig.1) might add to the LL s1, as well as some ss (repetitive $\text{sch}\sigma$).

The number of ad1 - new ones in spring x+2 and/or old ones from autumn x+1 (i.e. ad1 which remain adults without moulting in spring x+2) - often outnumber, more or less, the number of LL s1 or the number of all $\text{sch}\sigma$ (LL s1 + ? SL s1 + ss).

It is worth noting that in spring x+2 one does not compare males from the same year: in fact one compares ad1 and LL s1 which became, respectively, adults and intercalaries in two different years.

Even ad1 (e.g. belonging to stadium 7RO) collected in spring $x+2$ can be either males which became ad1 in spring $x+2$, or "old" ad1 which became 7RO adults the previous autumn: succession 7RO autumn ad1 7RO spring ad1 (Table 7).

TABLE 7. — Development and cycles of males of *T. niger* in Saarland and Burgundy, represented in a highly simplified way. Cases 1, 2, 3: starting from juvenile male (juv), with 6RO in summer/autumn (aut) $x+1$. - Cases 4, 5, 6: starting from juv or ad1, with 7RO in summer/autumn $x+1$. - Cases 7 to 12: males of the new generation (G) - i.e. ad1 or juv in spring $x+3$ - are represented. Only the case of LL sch♂ (and not that of SL ones) has been taken into account. Males from the generation of year $x-1$ have not been represented. First adults are underlined at the time they become ad1. Dashed line means a moult. Dotted line means no moult.

	autumn $x+1$		spring $x+2$			autumn $x+2$				spring $x+3$				autumn $x+3$		
	6RO	7RO	6RO	7RO	8RO	6RO	7RO	8RO	9RO	7RO	8RO	9RO	10RO	8RO	9RO	10RO
1	juv	-----	-----	<u>ad1</u>	-----	-----	-----	s1	-----	s1	-----	-----	-----	-----	ad2	-----
2	juv	-----	-----	juv	-----	-----	-----	<u>ad1</u>	-----	ad1	-----	-----	-----	-----	s1	-----
3	juv	-----	-----	juv	-----	-----	-----	juv	-----	-----	-----	<u>ad1</u>	-----	-----	-----	s1
4		juv	-----	-----	<u>ad1</u>	-----	-----	s1	-----	s1	-----	-----	-----	-----	ad2	-----
5		juv	-----	-----	juv	-----	-----	<u>ad1</u>	-----	ad1	-----	-----	-----	-----	s1	-----
6		<u>ad1</u>	-----	ad1	-----	-----	-----	s1	-----	s1	-----	-----	-----	-----	ad2	-----
7	(new G)									<u>ad1</u>	-----	-----	-----	s1		
8										juv	-----	-----	-----	<u>ad1</u>		
9										juv	-----	-----	-----	juv		
10											<u>ad1</u>	-----	-----	-----	s1	
11											juv	-----	-----	-----	<u>ad1</u>	
12										ad1	-----	-----	-----	s1		

In other words, in the case of LL, the intercalaries produced in summer/autumn of year "y" will not be "useful" for the reproduction which takes place in spring of the following year $y+1$. They will be able to reproduce - as ad2 - in spring of year $y+2$ (or in autumn of year $y+1$).

The above mentioned ad2 will add to the ad1 possibly produced in year $y+2$. When the new (= freshly) ad1 are few, we will observe situations like those found in Burgundy (France) near Chamboeuf and in the "Combe de Sainte Foi" (SAHLI, 1989): in these sites the postadult males (mostly ad2) were well represented in spring 1988.

In order to better understand the difference between LL and SL, let us add the following comment: if we were in the presence of SL (instead of LL) produced in autumn of year y, the males could mate the following spring $y+1$, after becoming postadult males (instead of staying intercalaries).

Contrary to SAHLI's 1967 statement, LL s1 may sometimes outnumber ad1, in spring. Such a case has been observed in the forest glade of Segrois ("Sommière de Segrois" near Chamboeuf, Côte-d'Or, France), March 30-31, 1985. In this case, the number of ad1 produced in spring 1985 was low (the winter 1984-1985 was exceptionally cold).

Summer/autumn (Table 6 and Fig. 1) is the main (or even exclusive) "season" of sch♂ production (e.g. ad. sch♂) in Saarland (epigeal animals) and in Burgundy. At this time of the year, the s1 (which have just become sch♂) may outnumber the newly appeared ad1 under two conditions (Table 6): (a) if the number of newly produced ad1 is low and (b) if the new spring ad1 of year $x+1$ were well represented. Such a case was observed in Wadrill (15. 9. 1957).

TABLE 8. — Simplified table of the cycles in males (A, C) and females (B) of *T. niger* in Saarland and Burgundy (only some of all the possibilities are given). Among other things, one can see when ad1 males appear (9RO males have not been represented). The possibility of 3RO larvae in autumn of the year x is not indicated. In A brackets mean ad2 originating from SL. In C, generation x-2. ED = Egg Deposition, N.G. = New Generation. Dashed line means a moult. Dotted line means no moult.

ED	Autumn x	Spring x+1	Autumn x+1	Spring x+2	Autumn x+2	Spring x+3
A	4RO	5RO	6RO	7RO ad1	8RO sch♂ →	8RO 9RO 10RO sch♂ (ad2)
	5RO	6RO	7RO ♂ Juv	♂ Juv	ad1	ad1
				8RO ad1	9RO sch♂	9RO sch♂
				♂ ad1	sch♂	10RO (ad2)
B			6RO	7RO	7RO	
			7RO	8RO	8RO	
				N.G.	6RO 7RO	
C		ad1 7RO	sch♂ 8RO	sch♂ 8RO	ad2 9RO	ad2 9RO
		7RO	7RO	7RO	8RO 9RO	9RO
		ad1	ad1	ad1	s1 → ad2	ad2
					ss	ss
					(8RO)	(8RO)
					s1	s1

At low altitude in Saarland (epigeal animals) - and probably in different regions of Germany, like Eifel, Taunus, Hunsrück, Hesse - and in Burgundy, summer and autumn typically constitute the time at which sch♂ are produced in *T. niger* (case a). Consequently sch♂ may be well represented in autumn (SAHLI, 1967). But, paradoxically, this is not always the case - at least apparently. Thus the number of ad1 can prevail over that of s1 when, for instance, the autumn ad1 production (year x+1, Table 6) was good. Such a case was observed at Wadrill (30.9.1962). In other words, the number of new autumn ad1 can prevail over autumn s1 of year x+1 (Table 6) when the production of spring ad1 of year x+1 was low.

Until recently, we had not understood what really happens in nature in *T. niger* (SAHLI 1966, 1967, 1970). Tables 5-8 and Figure 1 allow us to explain all previous field observations and culture results.

In *T. niger* the predominance of LL Sch♂ over SL (case a) might correspond to a sexual rest period (Table 9) in females (in the sense that females cannot be fertilized each year) - a rest period of one or several years, during which females may elaborate new ripe eggs. In other words, a female "indirect iteroparity" (SAHLI, this volume) might be another *raison d'être* of LL sch♂ and repetitive ones, which are male forms able to withstand harsh conditions (SAHLI, 1991c). Nevertheless, another hypothesis can be put forward: a splitting up and spreading of ♀♀ ad1 (and of egg depositions) over several years might be possible - such a strategy has been called the "CAT strategy" in males (SAHLI, 1990b). The appearance of female ad1 (from a single generation) during several years has been considered in mediterranean *O. sabulosus* (SAHLI, 1991b).

TABLE 9. — *T. niger* in Burgundy and Saarland. Indirect iteroparity (hypotetically admitted) in females, combined with LL in males is represented. The year $x+1$ during which no egg deposition occurs, is labelled "sexual rest" period and corresponds to the time needed for a new egg production; sum/aut: summer/autumn.

x		x+1		x+2
spring	sum/aut	spring	sum/aut	spring
♂♂ ad1 -----	s1 -----	s1 LL -----	ad2 -----	ad2
♀♀ first egg deposition	ad1	"sexual rest" period		2nd egg deposition

BLOWER (1969) & coll. (1964, 1974, 1977) had the great merit to introduce the notion of female iteroparity in myriapodology. Nevertheless this is only an hypothesis, and not a well established fact. I have partly adopted BLOWER's idea, at least as a working hypothesis. SAHLI (1993) subdivided it into (a) a direct iteroparity (egg deposition occurs in two consecutive years) and (b) an indirect one (the first egg deposition is separated from the second by an interval of over 2 or 3 years). The possibility of an indirect female iteroparity - with presence of LL sch♂ and R ones - has been suggested (SAHLI, 1993) in the case of the Pyrenean cave blaniulid *Typhloblaniulus lorifer consoranensis*, particularly because of the low temperatures which exist in these caves. The same reasoning can be applied to *T. niger*, which lives rather in relatively "cold" regions. The South limit in France seems to be the Département de la Saône-et-Loire. This species can be found further south in France at higher altitudes (particularly in the south-west, in the Pyrenees). In spite of periodomorphosis, *T. niger* is far less adapted to a hot and dry climate (e.g. of the Mediterranean type) than *O. sabulosus*.

FIG. 2. — *T. niger*, A: at Wadrill (Saarland, Germany). A1: stadium and specific sexual (ad or sch♂) frequencies of adult males (solid) and intercalaries (open), respectively at each stadium, from stadia 7 to 12RO. [e.g.: in stadium 8RO: ratio 8RO ad1 ♂/all adult ♂ (184); or: 8RO sch♂/all sch♂ (92)]. The frequencies are established from 184 ad♂ and 92 sch♂, respectively, collected between September 1957 and 1963 (inclusive). A2: total frequencies of ad♂ and sch♂, established from 375 individuals (ad♂ + sch♂) collected between May 1957 and 1963 (inclusive) [e.g. ratio 7RO ad♂/375 or ratio 8RO sch♂/375]. B: at Cîteaux (Burgundy, France). B1: stadium and specific sexual frequencies of ad♂ (204) and sch♂ (115) collected in 1963 and 1964. B2: total frequency of ad♂ (204) and sch♂ (115), according to 319 individuals collected in 1963 and 1964.

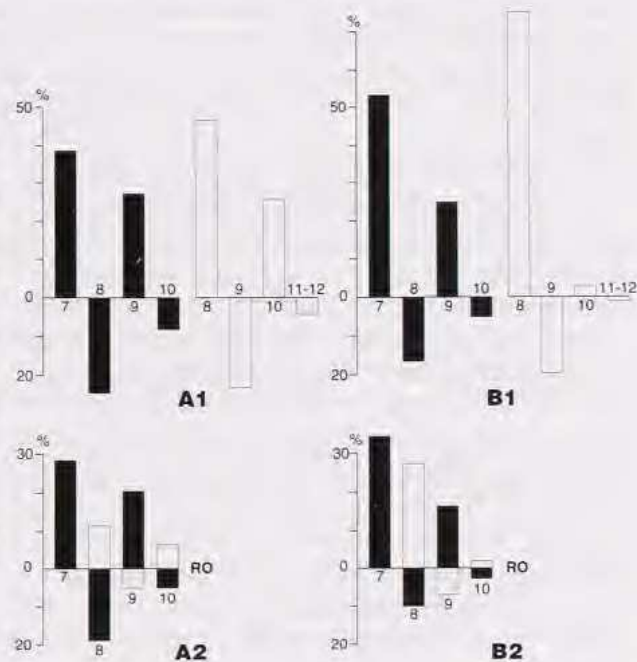


Figure 2 shows the ratios of adults and sch♂ at two Burgundy sites. Notice, particularly at Cîteaux (a) the lower percentage of s2 intercalaries (typically stadium 10RO when ad1 appear at 7RO) compared with the percentage of s1 (stadia 8 and 9RO) and, correlatively, (b) the lower

percentage of postadult ad2 males (a mixture of stadia 9RO males *pro parte* and possibly 10RO males *pro parte*). Drawing a parallel between ad2 and ad1 is in fact a comparison between animals which became adults at two different years; in this respect, one has to take into account the comment made before and Tables 5 & 6. Moreover, stadia 9 and 10RO may comprise not only ad2, but also ad1 (SAHLI, 1989). As for 12RO s3, they are very few: they imply some rare ad4 at both sites.

CONCLUSION

Taking into account the author's experimental results and observations, as well as those of VERHOEFF, in the present state of our knowledge, the following statements can be made. In good conditions and at low altitude in Burgundy and in Saarland, a majority of 7 and 8RO ad1 is able to turn into s1. The s1 are, in the majority, able to give either ad2 or ss. Then a fall seems to appear: only a part of the ad2 are able to turn into s2 and afterwards into ad3 - the relative importance of ad2 depends more or less on the temperature. A very low number of ad3 is able to give s3 and then ad4 (the number of s3 and ad4 seems to increase with altitude and depends on thermic conditions).

If one takes into account only the existence of LL all over the cycle and if the starting point for ad1 takes place in spring of the year y, then males will become ad4 in autumn of year y+4. If ad1 are 2 years old and possess 7RO, the ad4 might in theory be 6 years old, with 13RO; in the "Cirque de Gavarnie", in the Pyrenees at 2500m alt. and over, the oldest adult male with a ring formula of 72/2 (BROLEMANN, 1927) might belong to a stadium equivalent of 23RO (SAHLI, 1969).

Concerning *T. niger*, three comments will be added.

a) A possible dispersal - in time and space - variable for the male categories from one year to the next one, has to be taken into account. Spring sch♂ which became sch♂ the previous autumn y may have dispersed the year y in a given direction, while new ad1 which became adults in spring y+1 may disperse in another direction year y+1. In other words the dispersion areas in years y and y+1 might be different. So animal collections from a single locality may be biased.

b) Intercalaries can sometimes be more or less grouped or "gathered" (cf. SAHLI, 1991a in *O. sabulosus*). In Burgundy and Saarland *T. niger*, in spring and in case a, the activity of LL sch♂ and R individuals may be lower - because they do not moult in spring and do not search for females - than in new spring adult males. New spring adult ♂♂ are very active for two reasons (α) in spring they have just moulted (β) they move in order to search for females for spring mating (for an account of male activity in general, see SAHLI, this volume). FAIRHURST (1968) stated that, in Britain, *Tachypodoiulus* spring sch♂ - which, according to him, have just moulted in spring (= SAHLI's case b?; thus they might be SL - or ss?) - would, in spite of the moult, have a lower activity than spring adult males. FAIRHURST may be right. But field (or laboratory) experiments should be carried out. With experimental animals in equal numbers, the activity of fresh spring sch♂ (s1 -and not ss) should be compared with that of fresh spring ad♂ (ad1) in England and in *Tachypodoiulus*; if, under these conditions, there is a difference, then it can be attributed to sexual activity.

c) Due to the length of time of LL or R sch♂ states - thus to the long length of time between the appearances of ad1♂ and ad2♂ - it is not impossible that a loss of individuals might occur. If a loss really happens, it might be higher in LL and R sch♂ of *T. niger* than in SL of Mediterranean *O. sabulosus*.

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